Prospecting in a solitary breeder: chick production elicits territorial intrusions in common loons

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In many species, young animals learn about various breeding patches in one year and use what they have learned to settle in a promising patch the next. Common loons (*Gavia immer*) seem good candidates for such prospecting as prebreeders and displaced breeders intrude frequently into breeding territories defended by monogamous pairs yet engage in no extrapair copulations. We tested 3 hypotheses for prospecting in loons. The permanent attributes hypothesis gained little support as we found no consistent differences in quality between territories and no physical or biotic trait that predicted reproductive success in a territory. We found some support for the conspecific attraction hypothesis as intruders were attracted to conspecifics in a lake in the short term; however, intrusions were not more frequent in territories that had experienced regular use by a pair the previous year than in territories that had previously been vacant. Instead, the increase in intrusion rate after a year of chick production supported the habitat-copying hypothesis, which states that floaters use the presence of chicks as a cue to target territories for future attempts at territorial takeover. Despite this system of prospecting, founding of new territories was common. One striking finding was the tendency of territorial breeders to conceal chicks from flying intruders, perhaps to avoid future territorial takeover. *Key words:* common loon, floater, habitat copying, prospecting, territory. *[Behav Ecol 17:881–888 (2006)]*

Possession of a territory is essential for reproduction in many animals (Jacobs 1955; Lack 1968; Robertson 1972; Schaller 1972; Stamps 1977; Reichert 1982; Rood 1986; Jaeger and Forrester 1993). Because many species must wait years before acquiring a territory after reaching adulthood (Zack and Stutchbury 1992), acquisition of a territory is a crucial link in the life history of territorial species. Considering the ubiquity of territorial behavior and its close relationship with fitness, it is surprising that the process of territory acquisition is poorly known (Greenwood and Harvey 1982; Stamps and Krishnan 1999).

Our ignorance of territory acquisition results partly from logistic problems. The process often occurs quite rapidly, so most instances of it are not observed (e.g., Arcese 1989; Ens et al. 1996). New recruits to territories monitored by researchers tend to be unmarked, hence of unknown age and origin (Smith 1978; Hogstad 1999; Danchin and Cam 2002). In addition, lack of a theoretical foundation has hampered investigation of territory acquisition.

A promising window into territory acquisition is the phenomenon of "prospecting" (Reed et al. 1999). Defined as assessment by nonbreeders of multiple potential breeding areas before settlement on a single one (Reed et al. 1999), prospecting occurs in many motile animals (e.g., marine invertebrates: Doyle 1975; fishes: Armstrong et al. 1997; carnivores: Woollard and Harris 1990; rodents: O'Donoghue and Bergman 1992), but especially in birds, owing to their capacity for efficient long-distance movement (Reed et al. 1999). The phenomenon has attracted renewed interest recently (e.g., Brown et al. 2000; Doligez et al. 2002), in part because of its relevance to population dynamics and conservation (Reed and Dobson 1993; Jones 2001). Prospecting usually takes the form of visits by intruders to successful breeding areas late in one breeding season and recruitment to those areas the following year (Cadiou 1999; Schjørring et al. 1999).

In general, 3 conditions are thought to characterize species that exhibit prospecting (Boulinier and Danchin 1997; Schjørring et al. 1999). First, high-quality breeding sites must be scarce, otherwise little useful information can be gained through prospecting. Second, reproductive success must be consistent enough over time that a good breeding area located by prospecting in one year remains valuable in the subsequent years (see also Brown et al. 2000). Third, annual survivorship must be high enough that the fitness lost during a year or two of prospecting can be recouped through acquisition and extended use of a good breeding area.

Because production of offspring is the goal of a prospector, the presence of young in an area provides a good indication of the quality of the area to the prospector (Boulinier and

Danchin 1997; Danchin et al. 1998; Schjørring et al. 1999; Brown et al. 2000; Doligez et al. 2002). Recently, authors have begun to refer to the presence of young or some other cue indicating reproductive success as "public information" (e.g., Danchin et al. 1998) and settlement of prospectors in areas where reproductive success is high as "habitat copying" (e.g., Danchin et al. 2001; Parejo et al. 2004).

Much of the prospecting literature to date comes from birds that breed in colonies of dozens to thousands of nesting pairs (Coulson and White 1956; Cadiou 1999; Schjørring et al. 1999; Brown et al. 2000). In such cases, specific cues that might induce young animals to select the area for breeding are difficult to pinpoint. Study of prospecting in solitary breeders offers a better opportunity to detect cues that young animals might be using to locate breeding territories (e.g., Doligez et al. 2002).

The common loon is a long-lived solitary breeder in which territorial intrusions are frequent and obvious (2–3 daily, on average; Piper et al. 2000). Neither are intrusions aimed at extrapair copulation, which is absent in loons (Piper, Evers, et al. 1997), nor do they occur because of a need to forage, as intruders rarely do so (Piper, Paruk, et al. 1997). In addition, intrusions often elicit territorial vocalizations and physical defense by territorial residents and sometimes culminate in evictions of residents by intruders (Piper et al. 2000). Hence, this species offers an opportunity to focus on intrusions as efforts to learn about and usurp established territories.

Four classes of loons might potentially engage in prospecting behavior—1) "prebreeders": young individuals with no breeding experience (Cadiou 1999); 2) nonbreeders: those that have bred in years past but have been evicted from or abandoned a previous territory; 3) failed breeders: paired adults that have laid eggs during the year but not produced chicks; and 4) successful breeders: those that have chicks in the current year. For consistency with the literature, we shall refer to prebreeders and nonbreeders, collectively, as "floaters" to indicate that they are mature individuals not defending breeding territories (Smith 1978; Zack and Stutchbury 1992).

Several aspects of loon biology make investigation of territorial behavior and intrusions feasible. First, loons are conspicuous by virtue of their large size (females: 3.62 ± 0.22 kg SD, $N = 233$; males: 4.52 ± 0.30 kg, $N = 239$), their striking black-and-white plumage, their tendency to vocalize frequently, and the absence of visual obstructions on lakes they inhabit. Second, most territories (67 of 72 study lakes; 93%) consist of entire small lakes that intruders must enter in flight, making their detection by the territorial pair and human observers straightforward. Third, pairs remain in close association early in the breeding season (Piper, Evers, et al. 1997) and nearly always confront intruders (see Sjölander and Agren 1972). Finally, intrusions occur with greatest frequency in early morning (68% of all intrusions from 0500 to 0800) and late in the season (July and August), so observations focusing on these periods detect many intrusions.

We sought to use the loon system to examine 3 non–mutually exclusive hypotheses for territorial prospecting. The first, the permanent attributes hypothesis, maintains that prospectors aim to learn about permanent physical or biotic features of a territory that might serve as indirect cues of future breeding success there (see Brown and Rannala 1995; Badyaev et al. 1996; Brown et al. 2000). The hypothesis gives rise to 5 predictions: 1) chick production in a territory should be consistent across years, regardless of the adults breeding there; 2) some ecological cue or cues (e.g., lake size, depth, presence of islands, or availability of food) should be strong predictors of reproductive success; 3) the same cue or cues should be strong predictors of the rate of intrusion; 4) intrusion rates should be relatively constant from year to year because the features

themselves remain constant (Arcese 1989); and 5) prospectors should acquire vacant territories as well as occupied ones if territories themselves, not the presence or absence of breeders on them, is paramount.

A second hypothesis, the conspecific attraction hypothesis, posits that prospectors search for and settle near conspecifics to breed. Behavior of this kind could be adaptive, providing the presence of conspecifics in an area indicates a suitable habitat, permits group defense from predators, or facilitates mate attraction (Kiester 1979; Stamps 1987; Muller et al. 1997). Typically, conspecific attraction occurs when a naive animal settles to breed within an area already used by a cluster of breeding conspecifics (Stamps 1987). Because common loon territories are widely spaced, relative to breeding areas of many other species, use of conspecifics as a cue to good breeding areas can only take the form of evictions of established breeders rather than settlement near other breeders. As applied to the loon system, then, the conspecific attraction hypothesis predicts that 1) intruders are attracted to conspecifics they observe in breeding territories and 2) intrusions are more frequent on lakes used by pairs in previous years than on unused lakes.

A third alternative, the habitat-copying hypothesis, maintains that prospecting is aimed at specific cues that indicate reproductive success, like the presence of chicks. This version of habitat copying differs from others (e.g., Danchin et al. 1998; Schjørring et al. 1999) because it entails the use of cues from specific breeding pairs to recruit to specific territories. Consistent with this hypothesis is the finding that breeding loons are evicted from their territories with significantly greater frequency if they produced chicks there the previous year (Piper et al. 2000). Further predictions of the hypothesis are as follows: 1) consistency in reproductive success across several years but not necessarily over longer periods (Boulinier and Danchin 1997; Doligez et al. 1999; Brown et al. 2000); 2) intrusions into breeding patches during periods when information is available that might predict future breeding success there (e.g., visible chicks: Boulinier et al. 1996; Schjørring et al. 1999); and, most critically, 3) more frequent intrusions into territories that produced young the previous season (Boulinier and Danchin 1997; Cadiou 1999), which might represent efforts to confront and evict residents. Intrusions in the year of chick production are not expected because pairs with chicks defend territories with great intensity when they have chicks and because it is usually too late in the season to renest if chicks have already been produced there (WH Piper unpublished data).

Testing of predictions from the 3 hypotheses required us to focus on 2 main goals: analysis of predictors of intrusion and measurement of reproductive success in territories within and across years. In addition, robust evaluation of the hypotheses required data on territorial behavior of pairs toward intruders, consistency with which pairs occupied territories, and survivorship of pair members.

METHODS

Study area

We investigated territorial intrusion from 1993 to 2004 on 177 lakes (mean size ± SD = 50 ± 41 ha, range = 6–163) in Oneida County, Wisconsin, near the town of Rhinelander (center of study area: 45°40′N, 89°35′W). Our roughly 30 × 30–km study area consisted of second-growth forest containing coniferous (notably *Pinus resinosa*, *Pinus strobus*, *Tsuga canadensis*, *Abies balsamea*, and *Picea mariana*) and deciduous trees (including *Acer rubrum*, *Populus tremuloides*, and *Betula papyrifera*) interspersed with *Sphagnum* bogs and open water. The

region contains 386 lakes of sufficient size and quality to be used by loons for feeding and/or nesting including 5 of >500 ha, 26 of 100–500 ha, 34 of 50–100 ha, 44 of 25–50 ha, 91 of 10–25 ha, 75 of 5–10 ha, and 111 of 2–5 ha. The set of study lakes where we marked and studied loons increased from 12 in 1993 to 75 in 2004.

Study animal

The common loon, 1 of 5 congeners that procures aquatic prey by diving, winters along the southern coasts of North America and breeds across Canada, south into portions of 14 states of the United States of America. In northern Wisconsin, loons establish territories on lakes shortly after ice-out in April, lay 2-egg clutches in mid-May, and incubate jointly for 26–27 days. Early nesting failures, generally caused by mammalian egg predation (McIntyre 1975), are followed by 1–3 renesting attempts. Parents feed semi-precocial chicks on a diet of small fishes and aquatic invertebrates until they fledge, at 11–12 weeks (Barr 1996). Most loons acquire alternate plumage in their third year, at which point they return to the breeding ground (WH Piper, unpublished data). Age at first breeding ranges from 4 to 11 years (Evers et al. 2000). Hence, young adults, especially males, typically spend 2 or more years wandering in the vicinity of their natal lakes before establishing territories (Piper, Paruk, et al. 1997; Piper et al. 2000).

Capture and marking of loons

Many of our basic techniques have been described elsewhere (Evers 1993; Piper, Evers, et al. 1997; Piper, Paruk, et al. 1997). Briefly, we used motorboats to capture adults and chicks by nocturnal spotlighting from June to August of 1991–2004. Adults and chicks 6 weeks and older were given a single United States Fish and Wildlife Service band and 1–3 colored plastic bands (2-plex 1/16″, New Hermes, Inc., Duluth, GA) in distinctive combination. Reobservation of more than 2000 marked adults and chicks over a 10-year period suggests that neither capture itself nor the presence of leg bands substantially alters behavior or mortality (Evers 1993; WH Piper, unpublished data).

Behavioral observations of territorial pairs and intruders

From April through August of 1993–2004, single observers in canoes made visits to breeding lakes to look for intruders and monitor reproductive efforts of each pair. Most lake visits occurred between 0440 and 1200 and lasted at least 46 min (mean duration ± SD = 83 ± 27 min, N = 3159 visits). On the first visit of each year, we recorded the identities of pair members from leg bands using 10 × 50 binoculars. Thereafter, observers visited lakes at intervals of 2–7 days on a rotating basis. Observers noted all vocalizations and nesting behavior, found nests, and recorded the presence of young.

We recorded 3 kinds of evidence of extraterritorial loons. First, we recorded instances in which loons passed over a study lake in flight (flyovers). Second, we noted all occasions of outside loons physically landing (landings). Third, we recorded behaviors of pair members during these incursions, including any territorial yodels emitted by breeding males (Walcott et al. 1999; Walcott et al. 2006).

In addition to regular visits to 99 lakes defended by breeding pairs, we visited 78 lakes within the study area with no record of breeding the previous year. Visits to such undefended lakes occurred only once or twice each season, often after we had lost track of a banded bird from a defended lake or sought to check for a newly founded territory. Hence, some new breeding pairs were missed in their initial year together,

and others were not located until after they had been together for several weeks.

Statistical analysis

Our chief resource for testing hypotheses was a sample of 2891 separate early morning (starting time before 0900) visits by 19 observers to 99 breeding territories from 14 April to 30 August of 1993–2003. During this period, we recorded 2322 landings and 1607 flyovers. We regarded both flyovers and landings as territorial intrusions because both elicited territorial defense by pair members (most conspicuously the territorial yodel by males) and because flyovers were an effective means for intruders to observe breeders and chicks. However, we omitted from our sample all intrusions by successful breeders (see below), which might have occurred for reasons other than prospecting.

Intrusion rates were highly variable from lake to lake, probably because factors such as lake shape, size, location relative to large lakes (where floaters often feed), and lake quality varied in hard-to-quantify ways between lakes. Although we examined as many lake attributes as possible in examining the permanent attributes hypothesis, we tried to control lake effect on intrusion rates, when possible, by comparing intrusion rates within lakes between years for variables that differed between years. Hence, we performed paired t-tests on possible predictors of intrusion rate such as the presence or absence of chicks the previous year and the presence of a pair on the lake the previous year.

To analyze physical attributes as potential predictors of chick production, we used a least squares regression model with rate of chick production (proportion of years having produced chicks) as the dependent variable. Twelve chemical, physical, or biotic attributes of lakes measured by the Wisconsin Department of Natural Resources and potentially detectable by loon intruders were used as potential predictors: water clarity; pH of lake; maximum lake depth; abundance of muskie (*Esox masquinongy*), pike (*Esox lucius*), walleye (*Sander vitreus*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), or panfish (chiefly bluegill *Lepomis machrochirus* and yellow perch *Perca flavescens*); size of lake; presence or absence of islands; and "roundness" of lake (=perimeter in km divided by square root of area in ha). Backward elimination ($P < 0.05$ as criterion for retention) was employed to arrive at the best combination of predictors.

RESULTS

Identities of intruders

Our analysis of intrusions assumed that most intruders were searching for territories. However, most intruders were unmarked (1462 of 1961, 75%) and hence of unknown age and origin. Fortunately, we can infer the reproductive status of unmarked birds by looking at the 25% that were marked.

Among all intruders, 142 of 1961 (7%) were marked breeders from neighboring territories (see Piper et al. 2000) and 75 (4%) were marked nonbreeders that had been displaced from their territories. Breeders typically intrude into neighboring lakes (Piper, Evers, et al. 1997), and most lakes adjacent to a given study lake were also study lakes, owing to the large size of the study area, so most intruding breeders were from study lakes. Because a mean of 68% of all breeders were marked in study lakes, we can estimate that 7%/68% = 10% of all intruders comprised current breeders and 4%/68% = 6% were displaced breeders. Hence, roughly 84% of all intruders were prebreeders, whereas an estimated 90% were floaters. The sample of intruders analyzed to test the

hypotheses consisted of more than 90% floaters as we eliminated all marked current breeders from our sample.

The preponderance of prebreeders among intruders is affirmed by our data on loons banded as chicks that returned to intrude in the study area. Throughout the study, only 168 of 1961 intruders (9%) were marked 2- to 5-year-old floaters, but this segment of intruders increased from 19% of marked intruders (38 of 195) during 1993–1998 to 41% (123 of 299) from 2001 to 2003, owing to intensive banding of chicks in the study area that began in 1998. Considering that young floaters (especially females) often intrude into lakes many kilometers from their natal lake (Piper et al. 2000; WH Piper, unpublished data), we can be confident that most unmarked intruders were, in fact, prebreeders hatched outside of the study area.

Description of intrusions

Most landings follow a stereotyped pattern. Intruders fly over defended lakes, usually circling first and landing, often within 100 m of the pair. During landing, one or both pair members often emit a sharp "toot" call. After intruders land, pair members converge, lift their heads high above the water surface (the alert posture), and proceed rapidly toward the intruder by alternately swimming on the surface and beneath the water. Intruders approach pair members in a similar fashion. Once together, the 3 loons circle together with bodies 15–20 cm apart and heads bowed (the circle dance; Figure 2 in Sjölander and Agren 1972). At intervals during circle dances, 1, 2, or all 3 loons dive noisily, one after the other. Loons that remain on the surface "peer" under water constantly to track the movements of diving loons (see McIntyre 1988). On occasion, one loon (usually the intruder) flees from the others, propelling itself rapidly along the lake surface by flapping its legs and wings. Intruders usually depart soon after fleeing.

Permanent attributes hypothesis

Overall, our data provided limited support for the permanent attributes hypothesis. Two of 5 predictions gained tentative support, whereas one was supported strongly. 1) Proportion of years with successful hatch was not correlated between different pairs using the same territory (simple regression: $R^2 = 0$, $N = 25$ territories, $P = 0.96$; power to detect effect size of 0.5 [r] = 0.81). Hence, territories do not appear to exhibit permanent differences in the degree to which they support chick production. 2) Of the 12 chemical, physical, or biotic lake attributes (see above) examined as potential predictors of reproductive success, only the presence of islands weakly predicted long-term reproductive success of loons there (simple regression: $t = -2.65$, $R^2 = 0.13$, $N = 56$, $P = 0.01$). 3) The prediction that the presence of islands should also be a predictor of intrusions was not supported. When we controlled for the presence or absence of chicks the previous year (see prediction 3 under Habitat-Copying Hypothesis), territories with islands had rates of intrusion indistinguishable statistically from those without islands (chicks the previous year and islands: mean ± SD = 0.98 ± 0.52 intrusions/h; chicks the previous year but no islands: 0.99 ± 0.73; 2-sample $t = 0.04$, $P = 0.51$, df = 80; no chicks and islands: 0.78 ± 0.53; no chicks and no islands: 0.70 ± 0.47; $t = 0.69$, $P = 0.25$, df = 82). Power values for the t-tests were 0.95 and 0.99, respectively, presuming an effect size of 0.5 intrusions/h. 4) Intrusion rates were significantly, though weakly, autocorrelated between all consecutive years from 1994 through 1999 (simple regressions—1994–1995: $R^2 = 0.17$, $N = 26$ territories, $P < 0.05$; 1995–1996: $R^2 = 0.22$, $N = 40$, $P < 0.01$; 1996–1997: $R^2 = 0.09$, $N = 51$, $P < 0.05$; 1997–1998: $R^2 = 0.27$, $N = 50$, $P <$
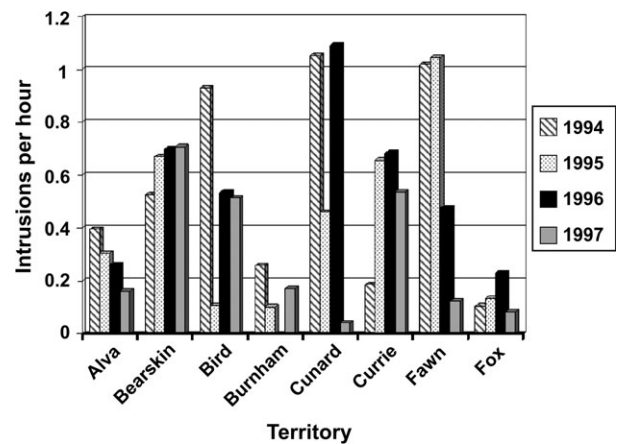
Figure 1
Rates of visits (intrusions and flyovers combined) for the first 8 study lakes alphabetically. Observations occurred chiefly from 0500 to 1200.

0.01; 1998–1999: $R^2 = 0.08$, $N = 53$, $P < 0.05$; Figure 1). 5) As predicted, nonbreeders acquired vacant as well as occupied territories. In fact, 55 of 170 (32%) territory acquisitions during the study period represented foundings of new territories, whereas 76 (45%) were by takeover and 39 (23%) by passive replacement of breeders that had disappeared and were presumed dead. The distribution of different modes of territory acquisition was identical in males and females.

Conspecific attraction hypothesis

One of 2 predictions from the conspecific attraction hypothesis was supported. 1) Floaters were strongly attracted to conspecifics. When no loon was present on the water, only 3% of all flying birds landed (2 of 70 events), whereas the frequency increased to 16% (34 of 218), 30% (163 of 552), and 51% (73 of 143), respectively, when 1, 2, and 3 or more loons were on the water ($\chi^2 = 77$, df = 3, $P < 0.001$). Similarly, the presence of a breeding pair on their territory was a strong predictor of visits by intrusions, both after a year of chick production (pair present: mean ± SD = 0.94 ± 0.53 intrusions/h; no pair present: 0.37 ± 0.57; paired $t = 6.2$, df = 54, $P < 0.001$) and after nest failure (pair: mean ± SD = 0.74 ± 0.49; no pair: 0.35 ± 0.56; paired $t = 4.3$, df = 54, $P < 0.001$). 2) Contrary to prediction, intrusions were not more frequent on lakes used by a breeding pair during the previous year (pair on lake previous year: mean ± SD = 0.69 ± 0.29 intrusions/h, df = 10; pair not on lake: 0.56 ± 0.55; $t = 0.75$, df = 10, $P = 0.47$). However, power was 0.7 (effect size 0.5 intrusions/h), indicating a good likelihood of failing to detect a real effect.

Habitat-copying hypothesis

Our data supported all 3 predictions of the habitat-copying hypothesis, including the critical prediction that chick production in a territory should result in a high rate of intrusions there the following year. 1) Territories with chicks in one year tended to produce chicks in years 2 (49 of 71 lakes, 69%) and 3 (37 of 58 lakes, 64%), whereas only 22 of 46 (48%) and 16 of 37 (43%) failed territories produced chicks in years 2 and 3, respectively (year 1 vs. year 2: Pearson = 3.8, $N = 117$, $P = 0.02$; year 1 vs. year 3: $\chi_1^2 = 3.9$, $N = 95$, $P < 0.05$). However, only 17 of 37 (46%) lakes with chicks in year 1 produced them in year 5, which did not differ from the 12 of 24 cases of chick
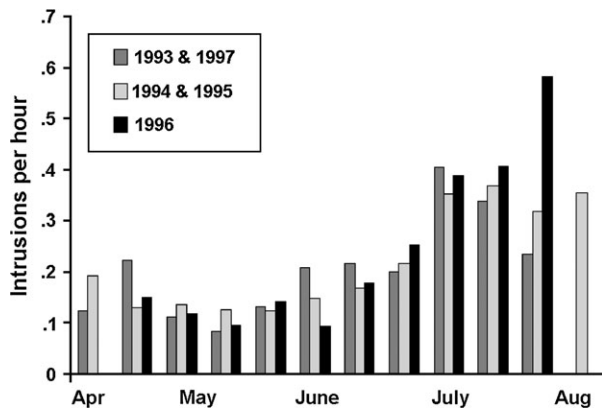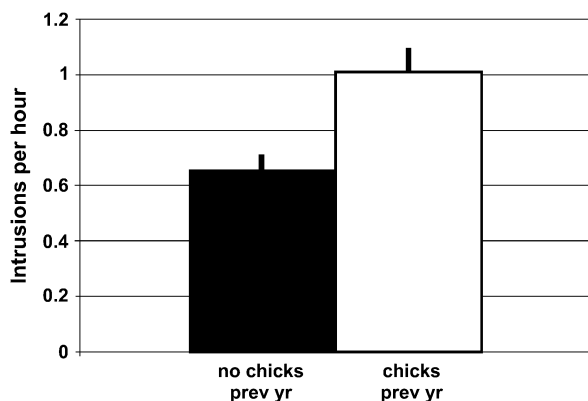
Figure 2
Mean rates of intrusions during the breeding season. Data were grouped by 10-day periods and years combined according to date of ice-out, which occurred on 27 April in 1993 and 1997, on 18 April in 1994 and 1995, and on 7 May in 1996.

production in failed territories (Pearson $\chi_1^2 = 0.1$, $N = 61$, $P = 0.78$). These results, together with those from prediction 1 of the permanent attributes hypothesis, show that territories differed in likelihood of producing chicks only over the short term. 2) As predicted, intrusions peaked in frequency during the period when chicks were present on the territory (Figure 2). The mean date of intrusions is also directly correlated with the date when ice comes off the lakes (simple regression: $R^2 = 0.78$, $N = 9$ years, $P < 0.01$) and hatching occurs ($R^2 = 0.71$, $N = 8$ years, $P < 0.01$). Thus, intruders' visits consistently track the chick-rearing period despite environmentally induced fluctuations in reproductive schedule. 3) The unique prediction that intrusions should be more frequent in years after chick production (mean $\pm$ SD $= 1.01 \pm 0.57$ intrusions/h) than after a year of failure (0.65 ± 0.37) was upheld (paired t-test: $t = 4.4$, df $= 57$, $P < 0.001$). On average, the intrusion rate was 54% higher in territories after a year of chick production (Figure 3).

Foundings of territories

As noted above, loons commonly founded new territories, in addition to claiming existing ones. By definition, founded territories were vacant before territorial settlement (usually for 5 or more years). Hence, no conspecific or reproductive

Figure 3
Mean intrusion rates ($\pm$SE) for 58 territories in years after chick production versus years after nest failure.

cue could have been used to determine where to found a territory.

Founded territories often produced chicks. Reproductive success of pairs in founded territories (19 of 53 hatched eggs, 36%) was somewhat lower than that in previously occupied territories (54 of 115, 47%), though not significantly so ($\chi_1^2 = 1.8$, $P = 0.18$, statistical power for this effect size $= 0.21$). Our estimate of reproductive success in founded territories is inflated because we did not systematically visit all vacant lakes in the study area early in the season to detect foundings but did survey such lakes for chicks each July. Thus, founded and previously occupied territories likely differ by a greater amount than our data show.

DISCUSSION

Foundings of territories

Loons commonly settle on new territories (see also Piper et al. 2000). Indeed, one might ask why a loon should ever compete for an established territory, at the risk of serious injury or death, when vacant territories are always available that are known to have produced chicks. Founding a territory has a relatively low energetic cost because it requires no confrontation of resident birds.

Despite the obvious fitness benefits to founding a territory, there are disadvantages as well. Founded territories produce chicks 31% less often than do established territories (a low estimate, see Results). Furthermore, there is a cost to founding territories because loons sometimes wait in a lake for several years, in hopes of attracting a mate, rather than prospecting in the local area for an established territory (WH Piper, unpublished data). Waiting on one lake rather than prospecting within an area containing many lakes might cost a loon a chance to learn of the disappearance of an established resident (see Ens et al. 1995; Bruinzeel and van de Pol 2004).

Regardless of the costs and benefits of founding, the system of territory acquisition in loons is clearly more complex than that reported for many species that exhibit prospecting. Within this group, loons appear to resemble oystercatchers, which employ a range of strategies to acquire a territory (Ens et al. 1993, 1995; Bruinzeel and van de Pol 2004). These include founding a new territory, replacing a dead resident on an established territory, and evicting a resident. Ens et al. (1995) and Bruinzeel and van de Pol (2004) argue that many oystercatchers join queues, establishing site-dependent dominance in local areas so that they can outcompete newcomers for occupied, high-quality territories in those areas. Although territories only vary in chick production over the short term in loons (see below), this species might exhibit a similar behavioral pattern. Clearly, young loons in search of territories focus their intrusions within a small area in the vicinity of their natal lake (Piper et al. 2000).

Assessment of hypotheses

Of 3 hypotheses tested for prospecting, the habitat-copying hypothesis gained the most support. Reproductive success was consistent across periods of a few years (e.g., Brown et al. 2000), revealing that information about reproductive success in one year is still useful in the next. Moreover, most intrusions occurred during chick rearing, a diagnostic pattern in prospecting species (Zicus and Hennes 1989; Reed et al. 1999; Schjørring et al. 1999; Tobler and Smith 2004) and a likely indication that intruders look for chicks at this time. Most importantly, intrusion rates increased greatly in years after chick production, suggesting that intruders targeted breeders on those lakes for eviction or passive replacement.

Use of reproductive cues by prospectors in one year to gain a suitable breeding site in the next has been confirmed for a growing number of birds, including many colonial breeders (Serventy and Curry 1984; Pickering 1989; Boulinier et al. 1996; Danchin et al. 1998; Schjørring et al. 1999; Brown et al. 2000; Dittmann and Becker 2003; Bruinzeel and van de Pol 2004; Tobler and Smith 2004) and some solitary breeders (Eadie and Gauthier 1985; Reed and Oring 1992; Doligez et al 1999, 2002; Ottosson et al. 2001; Amrhein et al. 2004). Typically, reproductive cues lead a prospecting individual merely to settle within a breeding colony or in the vicinity of the successful breeder it observed the previous year without interacting with other breeders there (e.g., Pärt and Doligez 2003). In a small but growing number of species, including loons, prospectors intrude to learn about and eventually claim breeding areas of specific established breeders, either by takeover or by passive replacement (Arcese 1987; Amrhein et al. 2004; Bruinzeel and van de Pol 2004). In cases where prospectors displace territory residents, breeders clearly suffer a severe loss in fitness as a result of prospecting.

The conspecific attraction hypothesis was supported in one respect: intruders were clearly attracted to adult loons within a territory. It is possible that loons searching for territories view both conspecifics and chicks as cues of where to settle. However, the situation is probably far simpler. Adult loons are conspicuous on the water by virtue of their contrasting black-and-white plumage; chicks, on the other hand, are a uniform chocolate brown in color and cryptic from lake level or above. Floaters, like human observers, probably use conspicuous adults to locate chicks. Indeed, use of adults to find chicks might explain an apparent inconsistency: flying intruders are attracted to adult loons in a lake but tend to revisit lakes the following year based on the presence of chicks, not adults.

A second possible explanation for the anomalous conspecific attraction we found is that, by approaching conspecifics, young intruders "parasitize" older birds with knowledge of chick production in the previous year (see Doligez et al. 2003). This leads to 2 predictions: 1) the intrusions of 3-year olds, which are in their first year on the breeding grounds and cannot be aware of the previous year's chick production, should be less well targeted toward previous chick production than those of older intruders and 2) 3-year olds should tend to join assemblages of intruders already present on breeding territories rather than initiating such assemblages. A growing number of marked, known-age intruders that result from intensive banding of chicks and limited natal dispersal will make these predictions testable in the next few years.

Countermeasures to prospecting

The fact that successful reproduction causes an increase in territorial intrusions and takeovers (Piper et al. 2000) raises the possibility that breeders might employ behaviors aimed at impeding prospecting. To our knowledge, no study to date has reported such behavior. Loons are good candidates for countermeasures to prospecting because they produce only 1–2 semi-precocial, cryptic chicks, which provide a relatively subtle indication of reproductive success, and because chicks can be moved about and hidden from prospectors.

Preliminary observations indicate that breeders might aim to deter prospectors in 2 distinct ways. First, the curious tendency of established breeders to intrude into neighboring territories might represent the effort by breeders to "decoy" prospectors away from their chicks. By leaving their breeding territories and intruding into neighboring territories, breeders with chicks probably reduce the likelihood of their own chicks being found (because prospectors appear to use adults to find chicks; see above). At the same time, visits of breeders with chicks to nearby territories increases intrusions by prospectors there instead of in the breeders' home territories.

A second countermeasure to prospecting appears to involve coordinated response of breeders and their chicks to flyovers. Once chicks reach about 4 weeks of age, adults and chicks begin to exhibit a stereotyped set of behaviors that we term "dive and scatter." After a flying intruder is spotted, the pair or lone parent dives and swims under water toward the center of the lake, whereas the chicks dive and swim under water toward shore. Once there, chicks hide among logs and rocks that they resemble until intruders depart. On observing the obvious adults near the middle of the lake, intruders invariably land near and approach them, ignoring chicks. In many cases, the behavior of breeders and chicks might prevent prospectors from detecting chicks. However, the strong effect of chick presence on intrusions the following year indicates that prospectors often observe chicks despite these countermeasures.

The possibility that dive-and-scatter behavior of adults and chicks is an attempt to hinder prospecting is particularly intriguing because the chief fitness benefit to chicks is indirect. Once they reach 4 weeks of age, loon chicks are no longer in danger of being killed by intruding loons (which, however, do kill very young chicks commonly; McIntyre and Barr 1997; WH Piper, unpublished data). Hence, hiding from prospectors by older chicks has little impact on their survival. Deterrence of prospecting might increase a chick's indirect fitness by reducing intrusions and evictions of their parents the following year, which decrease parents' fitness.

CONCLUSIONS

This study affirmed the importance of chicks as a cue used by prospectors to locate suitable territories. To date, our data are correlative, which leaves open the possibility that some correlate of chick presence, such as the presence of a successful nest, the sounds of calls made by chicks, or parental behavior related to chick rearing, could be the actual cue used by prospectors. Furthermore, our data indicate that prospectors look for adults in order to locate the salient cue, chicks. At present, we are using decoys to conduct experimental tests of the potency of chicks and adults as cues.

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